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PROXIMATE AND LANDSCAPE FACTORS INFLUENCE GRASSLAND BIRD DISTRIBUTIONS

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Abstract. Ecologists increasingly recognize that birds can respond to features well beyond their normal areas of activity, but little is known about the relative importance of landscapes and proximate factors or about the scales of landscapes that influence bird distributions. We examined the influences of tree cover at both proximate and landscape scales on grassland birds, a group of birds of high conservation concern, in the Sheyenne National Grassland in North Dakota, USA. The Grassland contains a diverse array of grassland and woodland habitats. We surveyed breeding birds on 2015 100 m long transect segments during 2002 and 2003. We modeled the occurrence of 19 species in relation to habitat features (percentages of grassland, woodland, shrubland, and wetland) within each 100-m segment and to tree cover within 200–1600 m of the segment. We used information-theoretic statistical methods to compare models and variables. At the proximate scales, tree cover was the most important variable, having negative influences on 13 species and positive influences on two species. In a comparison of multiple scales, models with only proximate variables were adequate for some species, but models combining proximate with landscape information were best for 17 of 19 species. Landscape-only models were rarely competitive. Combined models at the largest scales (800–1600 m) were best for 12 of 19 species. Seven species had best models including 1600-m landscapes plus proximate factors in at least one year. These were Wilson's Phalarope (*Phalaropus tricolor*), Sedge Wren (*Cistothorus platensis*), Field Sparrow (*Spizella pusilla*), Grasshopper Sparrow (*Ammodramus savannarum*), Bobolink (*Dolychonix oryzivorus*), Red-winged Blackbird (*Agelaius phoeniceus*), and Brown-headed Cowbird (*Molothrus ater*). These seven are small-bodied species; thus larger-bodied species do not necessarily respond most to the largest landscapes. Our findings suggest that birds respond to habitat features at a variety of scales. Models with only landscape-scale tree cover were rarely competitive, indicating that broad-scale modeling alone, such as that based solely on remotely sensed data, is likely to be inadequate in explaining species distributions.

Key words: grassland birds; habitat fragmentation; landscape features; North Dakota, USA; spatial autocorrelation.

INTRODUCTION

Identifying the habitat requirements of birds is essential for protecting habitat to maintain populations of the species. Numerous studies have focused on the proximate habitats used by birds, describing features associated with, for example, the territories, song perches, or nest sites of breeding birds (e.g., Capen 1981, Cody 1985, Wiens 1989). While there is growing recognition that the extent or contiguity of habitat beyond nesting territories can affect bird distribution or abundance, few studies have investigated the relative importance of proximate and landscape-scale factors. Fewer still have sought to identify the scales at which different species respond to habitat (show patterns of selecting or avoiding habitat features) in the landscape.

Identifying the scales at which birds respond most strongly to landscape features would help clarify and explain effects of fragmentation on bird distributions. Scale information could also guide habitat management, ensuring that efforts are applied at appropriate scales. Identifying dominant scales of response also would be useful in predicting environmental responses in contrasting areas, such as agricultural areas and wooded landscapes. Finding the major scales of response might also provide insight into the mechanisms by which birds respond to their surroundings.

Much of the initial research on the influence of different scales on breeding birds has emphasized forest-dwelling species (Robbins et al. 1989, Terborgh 1989, Finch 1991). In that context, landscape-scale habitat fragmentation has emerged as an important factor influencing population levels (Thompson 1995, Wiens 1995, Villard et al. 1999, Rodewald and Yahner 2001) and reproductive success (Small and Hunter 1988, Donovan et al. 1995, Robinson et al. 1995, Manolis et al. 2002, Batary and Baldi 2004).

During the past decade, scientists have come to realize that grassland birds are in greater decline than most

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PLATE 1. The Sheyenne National Grassland supports a diverse community of grassland-nesting birds, including the Upland Sandpiper (*Bartramia longicauda*) and Wilson's Snipe (*Gallinago delicata*). Photo credit: Tom Finkle

forest species. Results from the North American Breeding Bird Survey (Robbins et al. 1986) indicated that grassland-nesting birds had a higher proportion of declining species than did any other avian guild in North America (Droege and Sauer 1994, Knopf 1994, Peterjohn and Sauer 1999; see Plate 1). Their population declines have been attributed largely to the loss, fragmentation, and degradation of breeding habitat (McNicholl 1988, Johnson 1996, Igl and Johnson 1997, Coppedge et al. 2001).

Past studies have demonstrated that extent and proximity of woody habitats affect the distribution of many grassland birds, with greater bird abundance where wooded cover is sparse in the landscape (Soderstrom and Part 2000, Best et al. 2001, Coppedge et al. 2001, Ribic and Sample 2001, Fuhlendorf et al. 2002, Niemuth 2003). Some species, such as loggerhead shrike (*Lanius ludovicianus*), can respond more to landscape-scale factors than to proximate factors (Michaels and Cully 1998). In some studies, landscape-scale factors in combination with proximate-scale factors have produced the best habitat selection models (Fletcher and Koford 2002). Other studies (e.g., Bajema and Lima 2001, Horn et al. 2002), in contrast, have not found effects of landscape-scale features, suggesting that landscape sensitivity varies with species, habitat, and study methods.

Several studies that investigated nested landscapes found that grassland birds responded to landscape factors at scales from 200 to 1600 m (Bergin et al. 2000, Soderstrom and Part 2000, Ribic and Sample 2001, Bakker et al. 2002). Each of these studies found one or more landscape factors and landscape scales that explained the distribution of some birds. For example, Ribic and Sample (2001) found that the distribution of Grasshopper Sparrows (scientific names are given in Table 3) was explained about equally well by two models: one included proximate vegetation features and two landscape variables at 200 m, and the other included proximate vegetation features and three landscape variables at 400 m.

These studies were done in largely agricultural environments, where grassland habitat is relatively limited and fragmented. In contrast, our study area was extensive and encompassed habitat ranging from open grassland to heavily wooded sites. Previous studies were also restricted to narrow suites of bird species common in farmlands, and they also combined proximate and landscape variables in explanatory models, without examining in detail the relative importance of these scales.

These considerations led us to develop three primary objectives: (1) to investigate the occurrence of grassland birds in relation to both proximate habitat characteristics and landscape features in a prairie-dominated landscape, (2) to compare the relative importance of proximate and landscape features in predicting the occurrence of grassland birds, and (3) to assess the scales at which woody habitat in the landscape is most influential in predicting occurrence of different species. We focus on species that use grassland habitat facultatively and that are presumed to be breeding in the study area. Breeding species are of particular concern to both ecologists and land managers who are interested in understanding what makes suitable breeding habitat.

Study design and independence of observations

Concerns about independence among observations arise in landscape-level studies. Because landscapes rarely have meaningful, discrete boundaries, it is often impossible to define a distance at which landscapes are statistically independent of one another. One issue is spatial autocorrelation, or similarity between sampling points that are near one another (Legendre 1993). For example, the landscapes surrounding two transects in close proximity may overlap considerably, and explanatory variables derived from these overlapping landscapes cannot be validly considered as independent. Ideally, sampling sites should be far enough apart to avoid spatial autocorrelation, but how far is far enough? Ensuring that study areas are nonoverlapping is often an unattainable goal. Greater distances give more assurance of independence among observations, but independence remains a question of degree.

The major risk associated with nonindependent observations is underestimation of error in models. When similar conditions are measured repeatedly, the degrees of freedom are overestimated and error is underestimated (Diniz-Filho et al. 2003). When hypotheses are tested on the basis of significance measures (e.g., $P < 0.05$), underestimating error greatly increases the risk of falsely rejecting a true null hypothesis. In this study, we instead take a model-ranking approach, which does not rely on statistical significance to reject variables or models. This approach assumes that many models may offer some explanation, and it does not lead to rejecting models or variables, only identifying the most influential ones. We use bird counts taken on consecutive 100-m segments within long (2–6 km) transects. These observations, and the explanatory habitat variables around these 100-m segments, are not independent, but our method of evaluating these data does not hinge on assumptions of their independence. Pan (2001) also applied information-theoretic methods to nonindependent data.

A second issue, multicollinearity, arises when nested scales are used. The area within 200 m of a transect is part of the landscape within 400 m, for example, so landscapes at the two scales cannot be considered independent and their effects on the response variable are difficult to distinguish. See Graham (2003) for a review of the topic. Investigators have addressed this issue in several ways. Some (e.g., Soderstrom and Part 2000, Ribic and Sample 2001) examined correlation coefficients between variables at different scales and used only those scales for which correlation was minimal. Others (e.g., Fletcher and Koford 2002) selected a single scale. Another strategy has been to analyze each scale separately but not compare the behavior of particular variables across scales (Bergin et al. 2000). Our approach to this problem was to define separate models for nested landscape scales, then rank those models to compare the relative influence of explanatory variables. Thus one model includes tree cover at 200-m radius, and a separate model includes percentage tree cover at 400-m radius. These models are then ranked to indicate the relative explanatory importance of tree cover at these different scales.

Methods

Study site

The Sheyenne National Grassland in southeastern North Dakota is the largest expanse of publicly owned tallgrass prairie in the United States The Grassland consists of two units: a North Unit comprising 27 244 ha of federal land intermingled with private land and a South Unit consisting of 1157 ha of federal land. The vegetation of the Grassland area is a mixture of tallgrass prairie, mixed-grass prairie, wetlands, and woodland. The land is used extensively for rotational cattle grazing. Soils are sandy, with dunes from the shores of Glacial Lake Agassiz interspersed with low, flat areas. Expansive temporary, seasonal, or semipermanent wetlands occur in low areas (Svedarsky and Van Amburg 1996). Barker (1974), Manske (1980), and Seiler and Barker (1985) described the vegetation of the area. Plant communities described by Seiler and Barker (1985) include, in addition to tallgrass prairie, mixed-grass prairie on rolling upland topography, bur oak (*Quercus macrocarpa*) savanna and quaking aspen (*Populus tremuloides*) stands on upland dunes, and sedge meadows and wetlands in low-lying areas (Fig. 1). Low (0.5–1 m) shrubs, primarily western snowberry (*Symphoricarpos occidentalis*), are scattered throughout the mixed-grass prairie. Riparian deciduous forest occurs along the Sheyenne River, which crosses the northern edge of the Grassland. Basswood (*Tilia americana*), cottonwood (*Populus deltoides*), and willow (*Salix* spp.) dominate this forest. With its diversity of vegetation types, Sheyenne National Grassland supports a rich variety of birds (Martin and Svingen 2003) and a diversity of landscape types minimially interrupted by human settlements or agriculture.

Field methods

Birds were counted along belt transects (Stewart and Kantrud 1972, Igl and Johnson 1997) that extended 2–6 km from east to west. In 2002, 30 transects were systematically located, 2.09 km apart, with a random starting coordinate. We selected this interval so that section lines, many of which are lined with trees, fences, and roads, would be neither over- nor underrepresented in our sample. One observer walked these transects slowly (1 km/h), noting all birds seen or heard on either side. Birds detected within 50 m were recorded separately from those observed 50–100 m from the transect line. In 2003, 28 different transects were surveyed, interspersed midway between the previous year's transects. A global positioning system (GPS) unit was used to divide transects into 100-m units and to record bird counts by these segments, which could later be geo-referenced to land cover data. Bird counts were

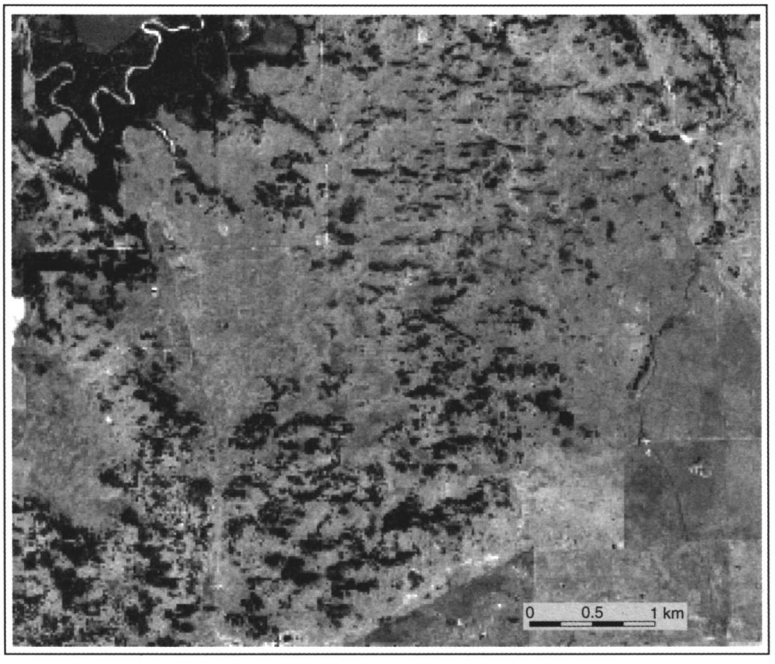

FIG. 1. Habitats in the Sheyenne National Grassland in southeastern North Dakota, USA. Riparian forest in the upper left contrasts with open savanna areas, which grade into open grasslands with stands of trees and temporary and seasonal wetlands. (Wetlands were mostly dry during the study.)

done between 0.5 h before sunrise and 4 h after sunrise, in winds <20 km/h and temperatures between 6° and 25°C, from late May to early July in 2002 and 2003. The same observer did surveys in both years.

The observer counted indicated breeding pairs. If sexes were alike, the number of singing males was counted. If no individuals were singing, then the number of observed individuals was halved and rounded up to derive indicated pairs. Brown-headed Cowbirds were recorded and analyzed separately by sex. Birds flying over the segment were included only if they apparently were using the area for foraging.

The observer also made visual estimates of vegetation cover (percentages in trees, shrubs, wetlands, and grass within 50 m and within 100 m of the transect line) on each 100-m segment. Wetlands were defined as any area currently or recently inundated that had wetland vegetation. Wetlands varied in size from a few hundred square meters to more than 50 ha. Most shrubs were 50–75 cm tall, but some willow thickets reached 2 m or more. Early in the breeding season, even low shrubs stood out prominently above herbaceous vegetation; later in the season, grasses and forbs reached the height of many shrubs, but the latter remained preferred song perches.

Because detectability differs by species and by habitat, and because we were considering multiple species in variable habitat, we used bird counts within a conservative distance of 50 m for all passerine species. We assumed that within 50 m detectability was reasonably consistent in different habitat conditions. Larger birds and shorebirds in the study area were highly conspicous, and initial analysis indicated that detectability was reliable at 100 m. Thus we used 100-m counts and vegetation estimates for all nonpasserine species. Because detectability varies among species, estimated occurrence or magnitude of effects should not be directly compared between species.

Landscape information

For landscape-scale habitat information, we used tree cover data digitized from 1-m resolution digital orthophoto quads (DOQs; U.S. Department of Agriculture, Natural Resources Conservation Service 2001). We used only tree cover because wetlands and shrubs were difficult to detect reliably on the DOQs, and ground-truthed observations indicated that available land cover and wetland data represented both shrublands and wetlands too inaccurately for habitat analysis. Past studies have shown that tree cover has important influences on habitat selection by grassland birds (Gates and Gysel 1978, O'Leary and Nyberg 2000), on nest success (Johnson and Temple 1990, Bergin et al. 2000), and on activity of some predators (Fritzell 1978, Winter et al. 2000). In our study area, unwooded areas were mainly grassland or grass interspersed with very low (<50 cm) shrubs, so the inverse of tree cover represented an approximation of the extent of open grassland habitat in a landscape.

While digitizing, we maintained spatial precision of at least 10 m. Digitized tree cover data were then converted to raster format at a cell resolution of 10 m. The GPS points were entered as point data in ArcGIS version 8.2 (ESRI 2002), and transect segments were digitized between GPS points. To calculate percentage of tree cover within nested buffers around these transect segments, we used an Arc macro language script in ArcINFO version 8.0.1 (ESRI 1999) to select each segment in turn; defined buffers around each segment at distances of 200, 400, 800, 1200, and 1600 m; and then clipped the tree cover grid data using these five buffers and exported the clipped "landscapes" to ERDAS image format for use in FRAGSTATS (version 2; McGarigal and Marks 1995). We then used FRAGSTATS to calculate percentage of tree cover for each buffered landscape surrounding each transect. Although FRAGSTATS produces many landscape fragmentation metrics, we used only percentage of cover, because this measure is more easily interpreted than other measures such as mean patch size or interspersion and juxtaposition indices. FRAGSTATS output was converted to a table listing percentage of tree cover at each buffer distance, and this table was merged with bird count data and vegetation data for analysis. Henceforth, we use "landscape variables" to refer to percentage of tree cover within the five buffer distances around the 100-m segments.

Statistical methods

We analyzed the presence/absence of each species within 100-m segments, using proximate and landscape-scale habitat as explanatory variables. The binary nature of the response variable lent itself to logistic regression, for which we used GENMOD, the generalized linear models procedure in SAS (SAS Institute 1996). At proximate scales (50- and 100-m distances from the transect line), explanatory variables included the percentage cover of trees (tree50, tree100), shrubs (shrub50, shrub100), grassland (grass50, grass100), and wetland (wetland50, wetland100). At landscape scales, explanatory variables were percentage cover of trees within 200, 400, 800, 1200, and 1600 m (tree200, tree400, etc.).

We ranked models using a multimodel inference approach (Buckland et al. 1997), rather than attempting to determine a single "best" model that described our data. Although the latter is a common strategy, it can lead to misinterpretation of results, especially when numerous or intercorrelated explanatory variables result in numerous models that fit the data nearly equally well. Instead, our aim was to rank the possible explanatory models and to retain all models that fit the data well. The assumption is that several models (and thus several variables) can have similar importance in explaining species occurrence.

We used an information-theoretic method to evaluate models (Burnham and Anderson 2002). We evaluated a prescribed set of models for their explanatory value and parsimony, then identified the strongest (best-fitting, most parsimonious) candidate models, based on low Akaike Information Criterion (AIC) values. For simplicity in comparing models, ΔAIC values were computed by subtracting the AIC value for the model with the lowest AIC value from the AIC value for each model. Then $\Delta\text{AIC} = 0$ for the "best" model and $\Delta\text{AIC} \geq 0$ for all other models. Burnham and Anderson (2002:70) gave a rule of thumb that models with ΔAIC of 2 or less may be considered competitive with the best model in explaining the response variable, while models with ΔAIC of 4 or greater are relatively poorly supported by the data. To be conservative in retaining potentially useful models, we considered models with $\Delta\text{AIC} < 3$ to be competitive.

Akaike weights were computed to indicate the weight of evidence, or probability, of a model from among those considered, based on the data observed. The Akaike weight for any model was proportional to $\exp(-0.5\Delta\text{AIC})$, and weights summed to one across all models considered. The relative influence of individual variables was assessed by summing the weights of the models in which each variable appears (Burnham and Anderson 2002:168). Comparing these variable weights helps avoid the risk of discarding variables that help explain bird distribution but do not appear in the "best" model.

We developed three suites of models to evaluate (1) proximate, (2) landscape, and (3) combined proximate and landscape effects for each species. In each case, we ranked models by running a model selection routine in SAS on groups of models, with each model consisting of one or more habitat or landscape variables. This routine calculated AIC, ΔAIC, model weights, and variable weights for each model and for each variable in the set of models. We performed all steps for each species separately. Because data were collected in two years and bird populations can change dramatically from one year to another, we included year and interactions between year and other explanatory variables in each model set.

We used three steps to identify competitive proximate models. First we ran the selection routine using a group of 16 models with the following explanatory variables: none (the null model); year only; year and each single habitat variable; year, each habitat variable, and the year $\times$ habitat interactions; and year with all two-way combinations of habitat variables. If a year $\times$ habitat interaction was included in one of the competitive models, all subsequent analyses were performed separately for the two years. Second, if multiple two-variable models were competitive, we added to the first model set three-variable models containing the variables with the greatest weights. Third, for species analyzed with 50-m bird counts, we tested whether 100-m or 50-m habitat variables better represented proximate conditions for a species: that is, we added to the model set a 100-m version of the best 50-m model. For example, if the best

TABLE 1. Range of values for explanatory variables at the Sheyenne National Grassland in southeastern North Dakota, USA.

Variable	Maximum	75% quartile	Median	25% quartile	Minimum
Grass50	100	90	70	50	0
Shrub50	90	30	10	0	0
Tree50	100	10	0	0	0
Wetland50	100	0	0	0	0
Grass100	100	80	70	50	0
Shrub100	90	30	10	5	0
Tree100	100	20	0	0	0
Wetland100	100	20	0	0	0
Tree200	77.5	11.2	1.4	0	0
Tree400	67.7	10.9	3.2	0.4	0
Tree800	50.8	10.5	4.5	1.6	0
Tree1200	46.4	10.7	5.2	2.2	0
Tree1600	46.4	11.8	5.2	2.7	0.1

Note: Variable names note habitat type and radius (for example, Grass50 represents the percentage of grass habitat within 50 m around transect segments).

model was (year + grass50 + wetland50), we added the model (year + grass100 + wetland100) to the set and reran the routine. From this step, we identified the strongest proximate models and variables for each species, at either 50 or 100 m.

We identified competitive landscape models for each species by running the model selection routine on groups of five or six landscape models. For species whose best proximate model involved 100-m variables, each landscape model included the percentage of tree cover at one of five scales (200, 400, 800, 1200, or 1600 m), as well as year (except where years were analyzed separately). For species whose best proximate model involved 50-m variables, we added a sixth landscape model incorporating tree cover at 100 m.

To compare the strength of proximate, landscape, and combined models in explaining species presence, we ran the model selection routine using the best proximate model, the five (or six) landscape models, and five (or six) combined models. Each combined model included the variables in the single best (lowest AIC) proximate model plus one of the landscape variables (tree100, tree200, tree400, tree800, tree1200, or tree1600). The tree100 variable was included only for passerine species, which were evaluated with 50-m count data. Year also was included in combined models, except when years were analyzed separately.

To identify the scales at which grassland birds respond most strongly to landscape configuration, we compared the magnitude of regression coefficient estimates for tree cover in the landscape-only regression models. To provide further insight into the scale findings, we also calculated each species' frequency of occurrence in relation to tree cover at different landscape scales. Using one scale at a time (e.g., 200 m), we grouped all observations by percentage of tree cover (tree200) and then calculated the frequency at which the species occurred in each tree cover class. Plots of frequency of occurrence against percentage of tree cover illustrate the nature and strength of the relationship.

We evaluated the goodness of fit of the best model for each species as follows. For each observation, we calculated the predicted response (1 for occurrence, 0 for nonoccurrence). We sorted the observations by these predicted values and then aggregated the transects into groups of approximately the same size (65, except for species analyzed separately by year, for which we used groups of 45). For each resulting group of transects, we calculated the mean predicted occurrence and the mean actual occurrence. We then computed a correlation coefficient between them as a measure of goodness of fit.

In addition to statistical analysis of species' responses to tree cover, we plotted incidence functions to show how observed occurrence of a species changed in response to increasing tree cover in the landscape. We did this process for each species at each landscape scale (200, 400, 800, 1200, and 1600 m). To create these plots, we sorted transect segments by percentage of tree cover at one scale, then aggregated the transects into groups of 20. For each group of 20 transects, we calculated a percentage of occurrences of a species, which we then plotted against the mean percentage of tree cover for that group. To avoid potential problems of correlations between habitat on the transect and woody habitat in the landscape, we restricted these incidence plots to only those transects on which proximate-scale tree cover was less than 10%. Thus all transects used were non-wooded and suitable for grassland birds, but the surrounding landscapes contained variable amounts of tree cover.

RESULTS

In two field seasons, we counted 9863 birds of 104 species in 2015 100 m long transect segments. Of the area surveyed, 63% of habitat was grassland, 18% shrubs, 11% trees, and 8% wetland. Landscape-scale tree cover ranged from 0% to 77% at 200 m, with decreasing percentages of tree cover at larger scales (Table 1). Correlations among nested landscape variables (tree cover at 200-1600 m) were strong ($r \geq 0.65$; Table 2). The proportions of habitat types on individual segments

TABLE 2. Correlations between explanatory variables (percentage of habitat types on transects or in the landscape).

Variable	Shrub50	Tree50	Wetland50	Tree200	Tree400	Tree800	Tree1200	Tree1600
Grass50	−0.51	−0.50	−0.48	−0.39	−0.35	−0.29	−0.26	−0.25
Shrub50		−0.12	−0.07	−0.08	−0.05	−0.03	−0.00	0.01
Tree50			−0.20	0.80	0.71	0.60	0.54	0.50
Wetland50				−0.19	−0.19	−0.18	−0.18	−0.17
Tree200					0.93	0.79	0.72	0.65
Tree400						0.92	0.84	0.76
Tree800							0.96	0.90
Tree1200								0.97

Note: Landscape-scale tree cover correlates closely with similar landscape scales; extent of wetlands and shrubs is not correlated strongly with the extent of trees in the landscape or on a transect.

were not strongly correlated with landscape-scale tree cover, except for tree cover, which was positively correlated with tree cover in the landscape. Habitat on adjacent segments was strongly correlated: correlation coefficients ranged from 0.59 to 0.73 for percentage of grassland, shrubland, woodland, and wetland on neighboring segments.

We analyzed the 19 grassland, wetland, or shrubland species detected on 30 or more segments during the two years (Table 3). For seven species (Mallard, Marbled Godwit, Marsh Wren, Vesper Sparrow, Bobolink, Western Meadowlark, and Brown-headed Cowbird), we conducted all analyses separately by year, because interactions between year and other explanatory variables contributed to competitive models. For the remaining 12 species we analyzed data from both years together but included a main effect of year in the models. Among best proximate models, tree cover on transects was the most common variable and frequently the heaviest-weighted variable. Best models also reflected the variables with highest cumulative weights across all models. Tree cover was important for 15 of the 19 species in at least one year. For 13 of these species, the response to trees was negative; for only Field Sparrow and Vesper Sparrow were responses positive. Wetlands also were frequently important, as many of the species were associated with wetlands. Grass and shrub habitats, the dominant, "background" habitat types, were less frequently important in models. Responses to grass were negative for Common Yellowthroat, Clay-colored Sparrow, male Brown-headed Cowbird, and, surprisingly, Upland Sandpiper and Bobolink (in 2002). These unexpected results may reflect the negative correlation between grass and trees at the proximate scale (−0.50; Table 2). In all other models for these two species, grass was positive.

Combined proximate and landscape models were better than proximate-only or landscape-only models for 17 of the 19 species (Table 4; for a graphic display, see Appendix A) and were competitive for the remaining two species, Mallard and Marbled Godwit. Seven species (Wilson's Phalarope, Sedge Wren, Field Sparrow, Grasshopper Sparrow, Bobolink in 2003, Red-winged Blackbird, and Brown-headed Cowbird) had best models at the largest scale examined in at least one year. An additional four had best models at 1200 m in at least one year (Wilson's Snipe, Marsh Wren in 2003, Clay-colored Sparrow, and Savannah Sparrow). None of these are large-bodied species. Some larger species, Blue-winged Teal and Marbled Godwit, responded to tree cover at shorter or mid-range distances. Mallards had no clear response to landscape features. Three species (Killdeer, Upland Sandpiper, and Red-winged Blackbird) had equivalent responses at both smaller and larger scales.

The best models fit observed data well, as indicated by goodness-of-fit values (Table 4).

Proximate and landscape model comparisons

Proximate-only models were competitive in at least one year for eight of the 19 species (Table 4). Thus proximate data alone could provide adequate information for nearly half the species discussed here. For the remaining 11 species, landscape data made meaningful improvement to the predictive power of models. Landscape-only models were competitive for one species (Marbled Godwit) in both years and for four species in just one year.

Among landscape scales, larger scales (800-1600 m) were the most frequently competitive (Appendix B). Nine species had competitive models only at these larger scales, in at least one year. Five species had competitive models only at scales less than 800 m in at least one year. Seven species had competitive models at a wide range of scales in at least one year.

Overall, combined models involving proximate variables and landscape variables at larger scales (>800 m) were competitive in at least one year for all species except Western Meadowlark. Models with proximate variables and landscape variables at smaller scales (≤800 m) were competitive for 11 of the 19 species in at least one year. Thus landscape scales >800 m provided useful information for a majority of species, but smaller landscape scales, as well as proximate information, also are important.

Species responding primarily to smaller scales (≤800 m) were Marbled Godwit and Western Meadowlark. Species responding generally to larger scales (≥800 m) were Wilson's Snipe, Wilson's Phalarope, Marsh Wren (in 2003), Field Sparrow, Savannah Sparrow, Grass-

TABLE 3. Species, number of transects on which species were detected (*N*), best proximate models, and individual variable weights.

Species	*N*	Best proximate model	Weights for variables in proximate models			
			Tree	Wetland	Grass	Shrub
A) 100-m species						
Mallard (*Anas platyrhynchos*) 2002	20	wetland100 + grass100	8	100	56	40
Mallard 2003	10	wetland100	42	78	25	24
Blue-winged Teal (*Anas discors*)	31	year + wetland100 − tree100	91	95	9	1
Killdeer (*Charadrius vociferus*)	63	year + wetland100 + grass100	4	100	99	12
Upland Sandpiper (*Bartramia longicauda*)	133	year − tree100 − grass100	100	24	72	1
Marbled Godwit (*Limosa fedoa*) 2002	18	−tree100 + wetland100	94	56	16	19
Marbled Godwit 2003	14	−tree100	92	22	21	17
Wilson's Snipe (*Gallinago delicata*)	35	year + wetland100 − tree100	92	95	9	2
Wilson's Phalarope (*Phalaropus tricolor*)	56	year + wetland100 + grass100 − tree100	91	100	91	0
B) 50-m species						
Sedge Wren (*Cistothorus platensis*)	53	year − tree50 + wetland50	100	62	58	1
Marsh Wren (*Cistothorus palustris*) 2002	18	+ wetland100	13	100	42	36
Marsh Wren 2003	21	−tree100 + wetland100 − grass100	87	89	39	34
Common Yellowthroat (*Geothlypis trichas*)	244	year − grass50 − tree50	97	3	100	0
Clay-colored Sparrow (*Spizella pallida*)	658	year − grass100 − wetland100	0	100	100	0
Field Sparrow (*Spizella pusilla*)	104	year + tree100 − wetland100	100	96	0	4
Vesper Sparrow (*Pooecetes grammineus*) 2002	39	+ tree100 + grass100	98	10	73	13
Vesper Sparrow 2003	40	+ tree100	100	18	18	17
Savannah Sparrow (*Passerculus sandwichensis*)	346	year − tree100 − shrub100	100	0	0	100
Grasshopper Sparrow (*Ammodramus savannarum*)	1028	year − tree100 − wetland100	100	100	0	0
Bobolink (*Dolychonix oryzivorus*) 2002	62	−tree100 − grass100	99	33	36	10
Bobolink 2003	53	− tree50	100	30	28	12
Red-winged Blackbird (*Agelaius phoeniceus*)	369	year − tree100 + wetland100	100	100	0	0
Western Meadowlark (*Sturnella neglecta*) 2002	148	−tree100	81	21	26	28
Western Meadowlark 2003	117	−tree100	37	23	34	22
Brown-headed Cowbird (male) (*Molothrus ater*) 2002	91	−grass50	24	26	63	44
Brown-headed Cowbird (male) 2003	63	−grass50	19	19	95	21
Brown-headed Cowbird (female) 2002	7	−wetland100 − tree100	45	52	37	27
Brown-headed Cowbird (female) 2003	18	−tree100 − shrub100	100	20	13	34

Notes: For best proximate models, variables and signs of coefficients (positive or negative effects) are shown. For example, the best proximate model for Marbled Godwit (*Limsoa fedoa*) in 2002 included a negative response to trees within 100 m and a positive response to wetlands within 100 m. Strengths of effects are indicated by cumulative weights. For 100-m species, we considered observations within 100 m of the transect line; for 50-m species, we used only observations within 50 m of the transect, to avoid risk of reduced detectability at greater distances. Variable weights are the cumulative Akaike weights of models in which a variable occurred. In general, the best proximate models include the most important variables. Where secondary variables have comparable weights, omitted variables may contribute to alternative competitive models. For species with an interaction between year and a land cover variable, all analysis was done separately by year, so year was not included in those models. For all other species, year was included in the models.

TABLE 4. Values of ΔAIC for proximate, combined, and landscape models.

Species	Proximate models		Combined models					Landscape models						GOF
	50 m	100 m	200 m	400 m	800 m	1200 m	1600 m	100 m	200 m	400 m	800 m	1200 m	1600 m	
Mallard (2002)		**0.0**	2.0	1.6	1.8	2.0	1.8	16.7	16.7	18.2	18.1	17.6	18.0	0.78
Mallard (2003)		**0.0**	2.0	1.7	1.8	2.0	2.0	4.0	6.8	7.4	7.3	7.2	6.9	0.34
Blue-winged Teal		0.8	1.7	**0.0**	2.5	2.8	2.6	17.4	17.1	14.1	22.3	25.4	24.5	0.89
Killdeer		2.4	2.9	**0.0**	1.4	1.1	0.2	31.2	26.0	21.2	26.1	26.7	25.9	0.93
Upland Sandpiper		3.8	0.8	**0.0**	3.7	4.0	2.5	11.5	12.1	14.6	32.1	37.1	36.8	0.76
Marbled Godwit (2002)		14.0	11.0	1.2	9.8	9.7	12.8	16.3	11.9	**0.0**	12.4	13.6	19.3	0.87
Marbled Godwit (2003)		13.8	12.4	6.9	2.0	4.0	7.2	NA†	10.4	4.9	**0.0**	2.6	6.8	0.71
Wilson's Snipe		10.2	6.7	6.7	3.8	**0.0**	1.1	19.7	13.5	14.3	12.6	13.0	9.9	0.83
Wilson's Phalarope		22.5	21.4	16.1	8.7	4.3	**0.0**	46.4	45.6	38.9	31.5	30.0	26.9	0.92
Sedge Wren	1.4	2.2	2.6	3.3	3.3	0.8	**0.0**	6.4	13.6	19.9	24.6	17.9	17.9	0.74
Marsh Wren (2002)	13.2	7.2	3.3	1.7	**0.0**	2.4	2.5	60.3	46.8	42.4	40.5	45.6	44.8	0.96
Marsh Wren (2003)	22.4	14.2	11.2	3.7	0.7	**0.0**	2.4	44.2	36.1	25.8	27.2	34.4	39.4	0.93
Common Yellowthroat	0.6	4.4	**0.0**	1.6	2.5	2.6	2.3	161.2	158.1	159.5	161.7	162.4	163.1	0.94
Clay-colored Sparrow	10.1	1.6	3.5	2.4	0.4	**0.0**	1.3	161.6	155.1	146.2	150.9	155.2	165.6	0.81
Field Sparrow	81.0	77.7	35.8	24.1	10.9	1.9	**0.0**	91.3	60.2	59.7	61.1	57.5	65.2	0.90
Vesper Sparrow (2002)	13.7	8.0	4.6	**0.0**	1.1	0.4	1.8	13.6	9.1	6.1	10.0	9.8	12.0	0.62
Vesper Sparrow (2003)	11.3	7.6	0.6	**0.0**	0.3	1.9	2.6	NA†	1.0	2.6	7.9	14.4	19.4	0.71
Savannah Sparrow	91.1	61.7	19.2	7.9	2.2	**0.0**	8.3	88.2	58.5	64.4	85.2	97.4	124.5	0.96
Grasshopper Sparrow	24.2	18.7	12.8	20.7	14.1	6.6	**0.0**	81.8	125.6	198.3	264.1	286.1	301.0	0.95
Bobolink (2002)	1.1	0.1	0.0	1.4	1.7	1.9	1.9	1.4	0.1	3.9	11.1	11.0	11.6	0.82
Bobolink (2003)	1.5	4.6	3.3	3.5	2.4	2.0	**0.0**	4.6	10.2	17.8	25.5	27.4	30.0	0.81
Red-winged Blackbird	46.6	27.0	6.3	2.0	12.7	8.3	**0.0**	185.1	157.8	155.5	193.2	196.6	191.4	0.92
Western Meadowlark (2002)	17.3	14.7	**0.0**	2.3	5.2	7.9	10.3	14.7	0.4	0.8	3.3	6.6	9.9	0.66
Western Meadowlark (2003)	30.4	28.8	**0.0**	10.2	21.4	19.9	21.1	28.8	6.2	10.1	19.6	18.4	20.1	0.71
Brown-headed Cowbird (male) (2002)	5.4	6.6	4.3	3.5	3.0	1.2	**0.0**	11.2	11.1	10.7	10.1	8.9	7.9	0.49
Brown-headed Cowbird (male) (2003)	5.8	8.5	7.8	7.6	5.1	3.4	**0.0**	15.9	16.1	17.4	16.3	15.1	12.3	0.77
Brown-headed Cowbird (female) (2002)	2.7	1.4	2.2	2.0	2.1	1.3	**0.0**	4.5	3.9	4.2	4.8	4.1	2.7	0.75
Brown-headed Cowbird (female) (2003)	19.1	15.3	17.2	17.1	12.9	6.8	**0.0**	15.3	24.7	27.7	20.6	13.8	6.5	0.95

Notes: The best explanatory models for presence/absence of a species (ΔAIC = 0; boldface type) were at scales of 1200–1600 m for 11 species in at least one year; most of these were small-bodied species. Some species (e.g., Wilson's Phalarope, Brown-headed Cowbird) showed declining ΔAIC values with larger scales even for landscape-only models. Goodness of fit (GOF) shows correlation between grouped observed and predicted occurrence values (see *Methods*).

† For these species, the best proximate model included only trees at 100 m, so that the 100-m landscape model was the same as the best proximate model.

hopper Sparrow, Bobolink (in 2003), and both sexes of Brown-headed Cowbirds. Species responding equally (either strongly or weakly) to both large and small scales were Mallard, Blue-winged Teal, Killdeer, Upland Sandpiper, Sedge Wren, Marsh Wren (in 2002), Common Yellowthroat, Clay-colored Sparrow, Vesper Sparrow, Bobolink (in 2002), Red-winged Blackbird, and female Brown-headed Cowbird (in 2002).

Regression coefficient estimates demonstrated the strength of tree cover effects across scales (Appendix C). In general, scales that produced small ΔAIC values in landscape models corresponded to the scales with large parameter estimates.

Incidence plots

Plots of observed incidence showed the rate of occurrence of a species in response to tree cover (Fig. 2). All incidence plots were based on only treeless transect segments, so that at a proximate scale all should be similarly suitable for grassland species. For most species, these plots showed fewer birds in wooded landscapes. For example, the probability of observing Savannah Sparrows on a transect fell from nearly 30% to <10% as the amount of tree cover within 200 m increased from 0% to 18%. This trend persisted for larger landscapes. Incidence plots showed similar decreasing occurrence at large scales for six of the nine passerine species that tended to avoid tree cover (Sedge Wren, Marsh Wren, Savannah Sparrow, Western Meadowlark, Red-winged Blackbird, and Brown-headed Cowbird). Because all incidence frequencies were calculated using only those transects with <10% tree cover on the transect itself, this pattern does not reflect a correlation between small and large landscapes. Two additional passerine species (Common Yellowthroat and Vesper Sparrow) tended to occur near trees and showed increasing occurrence rates as tree cover increased in the landscape. One species, Vesper Sparrow, did not occur on transects with <10% tree cover.

DISCUSSION

Habitat selection is a poorly understood process, despite the considerable research devoted to it (Jones 2001). The main focus has been on proximate features such as the vegetation within a territory. More recently, attention has turned to the entire habitat patch in which

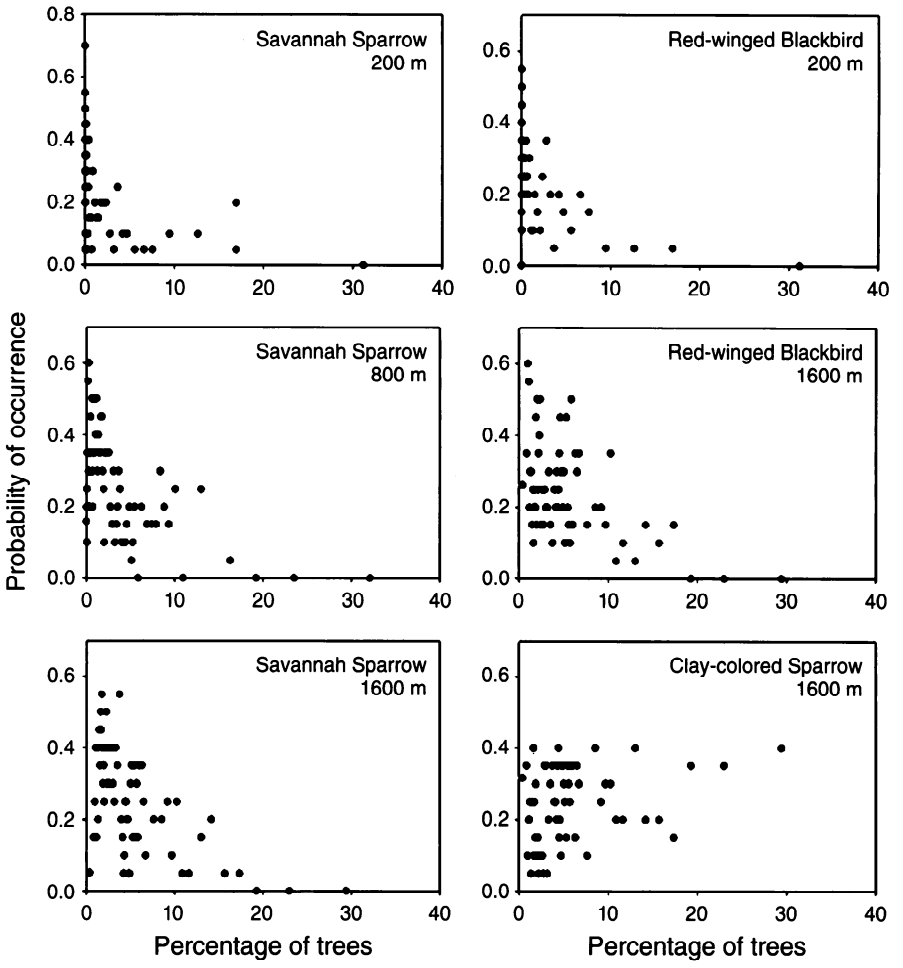

FIG. 2. Incidence functions show that the probability of occurrence decreases with increasing percentage of trees in the landscape. Each graph shows bird occurrence by percentage of tree cover at one scale (200, 800, or 1600 m from a transect). For Savannah Sparrow, Red-winged Blackbird, and four other species, this pattern persisted for landscapes of 1600 m radius around transects. Plots represent only transects on which proximate-scale tree cover was <10%; we excluded wooded transects because tree cover at proximate and landscape scales are often correlated, and we wished to avoid confounding effects of proximate and landscape factors. For three species, including Clay-colored Sparrow, incidence increased with the amount of tree cover in the landscape, even when assessed at large scales. Probability of occurrence (y-axis) differs between graphs because dots represent groups of observations that were sorted by percentage of the explanatory variable and then aggregated into groups. Because the groupings varied by scale, groups at some scales had higher incidence than at others.

a territory is located and the landscape in which those patches are embedded. Our study area provided an ideal system to investigate factors that influence habitat selection in birds, because it included a wide range of habitats and landscapes, from completely open grassland, through mixed savanna-like fields, to nearly closed-canopy woodlands.

A majority of the investigated species responded to habitat at both small and large scales, so that combined models, incorporating both proximate habitat and landscape features, were good for all species. The benefit of combining proximate and landscape scales has been noted by others (e.g., Fletcher and Koford 2002). However, taken alone, proximate-only models were much more useful than landscape-only models. Proximate models were competitive for nearly half the species discussed here, which emphasizes the importance of local habitat conditions.

Large-scale landscapes were important, even though they provided poor predictive power when taken alone and even though we included only tree cover. For several species, such as Savannah Sparrow and Grasshopper Sparrow, large-scale landscape-only models were poor, but those landscape features contributed to very good combined models. Thus, larger landscapes added more independent information to the proximate model.

Influential landscape scales extended far beyond nesting territories. For example, Sedge Wrens, Clay-

colored Sparrows, Savannah Sparrows, and Grasshopper Sparrows were best predicted by combined models that included tree cover at 800-1600 m (Table 4; Appendix A). Yet the nesting territories defended by these species typically ranges from 0.5 to 2 ha (Fox 1961, Salt 1966, Root 1968, Burns 1982, Dechant et al. 2003*a*, *b*).

Goodness-of-fit results show that our models predicted most species well. Species with poorer fits included some ubiquitous species (Western Meadowlark, Brown-headed Cowbird) as well as uncommon species (Marbled Godwit), which were frequently absent from apparently suitable habitat.

Species analyzed separately by year had generally similar responses across the range of scales (Appendix A), even though some of these species had very few occurrences each year. Even where proximate models differed, the scale of strongest landscape response was the same or similar in both years. These results suggest that, at least with a large number of sample points, a small number of detections may still produce a reliable pattern.

Results from comparable studies

In comparison to other studies that used nested scales to evaluate landscape responses in grassland birds, our results show some similarities and notable differences. Consistent with our results, large-scale landscapes have been found important for Sedge Wrens in Iowa (Fletcher and Koford 2002) and South Dakota (Bakker et al. 2002), while Grasshopper Sparrows showed relatively weak landscape responses but strong responses to a combination of proximate and landscape features (Ribic and Sample 2001, Bakker et al. 2002, Fletcher and Koford 2002). Like us, Fletcher and Koford (2002) found proximate influences dominant for Common Yellowthroats. Bobolinks have shown relatively strong responses at proximate scales (Bakker et al. 2002), but Ribic and Sample (2001) found that Bobolinks showed stronger responses to landscapes at 800 m in southern Wisconsin.

In contrast to our study, Bakker et al. (2002) found large-scale landscape responses in Clay-colored Sparrows, where we found none. For Savannah Sparrows, Ribic and Sample (2001) found 800-m landscape responses most influential, we found stronger responses at 200–400 m, and Bakker et al. (2002) found no landscape features that improved their models. For Western Meadowlarks, our results showed little effect of proximate conditions, while Bakker et al. (2002) found strong effects of proximate features and little landscape effect.

Most influential habitat variables

At the proximate scale, trees exerted more effect than any other habitat variable. Most species responded negatively to the presence of trees. Exceptions were Mallard and Killdeer, both wetland species that appeared indifferent to tree cover at proximate scales, as well as Field Sparrow, Clay-colored Sparrow, Vesper Sparrow, and male Brown-headed Cowbirds, all of which use woody vegetation as well as grassland habitats for various activities (Hahn and Hatfield 1995, Rising 1996). Other investigators also have found that proximity to woody vegetation is important in explaining the occurrence of some species (Coppedge et al. 2001, Bakker et al. 2002, Fletcher and Koford 2002), as well as nest predation (Stephens et al. 2004).

The apparent lower importance of shrubs, grass, and wetland at the proximate scale may be due partly to the way these habitat types grade into each other. Whereas trees stood out distinctly from the surrounding vegetation, wetlands (many of which were dry) differed relatively little in structure from surrounding grassland. Also, many wetlands were small and lacked open-water areas that might have deterred grassland species. Many of the shrubs were little taller than the surrounding herbaceous vegetation, and they were often widely scattered, rather than clustered. As a consequence, shrubs often contrasted little from the herbaceous vegetation.

Most wetland-dependent species, not surprisingly, were positively influenced by the presence of wetland in a segment, but most of our wetland species also showed landscape-scale responses to tree cover. Habitat selection of wetland birds is usually assessed in terms of the numbers, sizes, and types of wetlands (e.g., Weller and Spatcher 1965). The wetland birds' avoidance of tree cover is not because wetlands occur away from trees: correlation coefficients (Table 2) indicate that there is little relationship between the presence of these two habitat types in the landscape. Naugle et al. (2001) similarly found that Wilson's Phalaropes and certain other wetland bird species were influenced by features of the landscape surrounding wetlands. On a more local scale, Naugle et al. (1999) observed reduced occurrences of Wilson's Phalaropes and Red-winged Blackbirds but greater occurrences of Marsh Wrens on wetlands surrounded by more trees; we found that all three of these species were less frequent on segments with greater tree cover. Wetland-dependent species, then, may be susceptible to double threats from habitat degradation: both wetland loss and tree encroachment into grasslands may reduce the quality of available breeding habitat.

Most influential landscape scales

For 11 species in at least one year, the lowest AIC values for combined or landscape-only models involved variables measured at 1200–1600 m. Three of these (Wilson's Snipe, Wilson's Phalarope, and Brown-headed Cowbird) are wide-ranging species. One (Field Sparrow) tends to prefer partially wooded environments and usually occurred in trees. The remaining species that showed sensitivity to the largest landscapes were small, territorial species generally presumed to remain near nest sites in open grasslands, wetlands, or shrublands.

Some large, mobile species (Upland Sandpiper, Marbled Godwit, and Blue-winged Teal) showed strongest responses to trees at smaller scales. Thus large and wide-ranging species are not necessarily the most sensitive to the largest landscapes. While these larger birds frequently selected landscapes at small or mid-range scales, small passerine species (e.g., Field Sparrow, Grasshopper Sparrow) often responded to wooded landscapes even at the largest scales measured here. Thus body size did not explain large-scale landscape responses.

Many previous studies of landscape responses in grassland birds have used landscape variables described within 1000 m or less of study sites. Scales of <1000 m were most useful for about half our species. The other half of our species had strongest responses beyond 1000 m, indicating that future studies of these species should include larger scales.

Model ranking and habitat selection

A key assumption of the approach we followed is that a number of plausible explanations for a relationship may exist. Several of the species had two or three competitive proximate models, and most had several combined models that were competitive. While it is tempting to identify a single "best" scale for each species, we found that that models at very different scales provided nearly equivalent AIC values for some species, such as Killdeer (400 and 1600 m), Grasshopper Sparrow (200 and 1600 m), and Marsh Wren (200–1600 m). The existence of multiple useful models underscores the fact that analytical methods designed to select a single best model, as in stepwise regression, can easily be misleading (Pope and Webster 1972, Hurvich and Tsai 1990). These methods eliminate alternative, competitive models, perhaps inappropriately, as they identify a single best model. Studies seeking to compare variables at different scales will provide the most useful conclusions if they present results at a range of scales, rather than presenting the single best set of explanatory variables.

Comparing AIC values only tells the *relative* value of models, not their actual predictive ability, but goodness of fit was strong for our best models. For those species evaluated separately for 2002 and 2003, comparisons across scales and variables were similar in both years. Even for species with few detections, responses to scales and to habitat variables were consistent. Although van Belle (2002) recommended at least 10 events (occurrences) per explanatory variable included in a logistic model in order to produce reasonably stable estimates of parameters, we found realistic and consistent patterns even with small counts.

Management and research implications

Understanding scales of response to tree encroachment in grasslands will be helpful in monitoring and managing habitat for grassland birds. In many conservation areas, landscape-scale factors are beyond managers' direct control, but information about surrounding landscapes may be useful in understanding more proximate changes in populations. In some areas, such as the Sheyenne National Grassland, managers have the opportunity to manage large-scale landscapes, so more information on which species respond at which scales will contribute to management efforts. In grasslands, tree cover may be perceived by some individuals as attractive because it increases local bird diversity, but where management is aimed at improving conditions for grassland species, tree removal is likely to be an important strategy. Land managers may also consider focusing on habitat availability in the landscape, rather than just habitat patch size, in monitoring species distributions or managing populations.

Sample sizes are often limited in landscape-scale studies because of concerns about spatial autocorrelation. It is important to be cautious about spatial autocorrelation when analyzing data, but meaningful and repeatable results may be derived from data that do not meet assumptions of independence if hypothesis-testing methods are avoided. Information-theoretic methods such as model ranking and model selection are increasingly important in ecological studies, and, while autocorrelation remains an important consideration, its risks do not outweigh the benefits of large sample sizes.

Attention to both proximate and landscape-scale features is important in studies of habitat selection. Researchers working in small study areas should acknowledge the larger-scale context when interpreting habitat selection; and landscape-oriented habitat modeling efforts should attend to local conditions. Where landscape-scale studies rely on remotely sensed data, it is important that methods and data give reasonable insights into habitat conditions at 400- to 800-m scales, not just at larger scales. Regional-scale modeling of habitat availability should be considered effective for the types of large-scale responses we have found here. But it should be remembered that for most species these large-scale data are most useful in combination with local-scale information. Habitat modeling at regional scales should be done on the assumption that only part of the story, and a relatively small part at that, is being told.

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APPENDIX A

Plots of ΔAIC show scales of response and comparisons between years, as well as comparisons between proximate, landscape, and combined models (*Ecological Archives* A016-039-A1).

APPENDIX B

A table providing a summary of scales at which models are competitive for each species (*Ecological Archives* A016-039-A2).

APPENDIX C

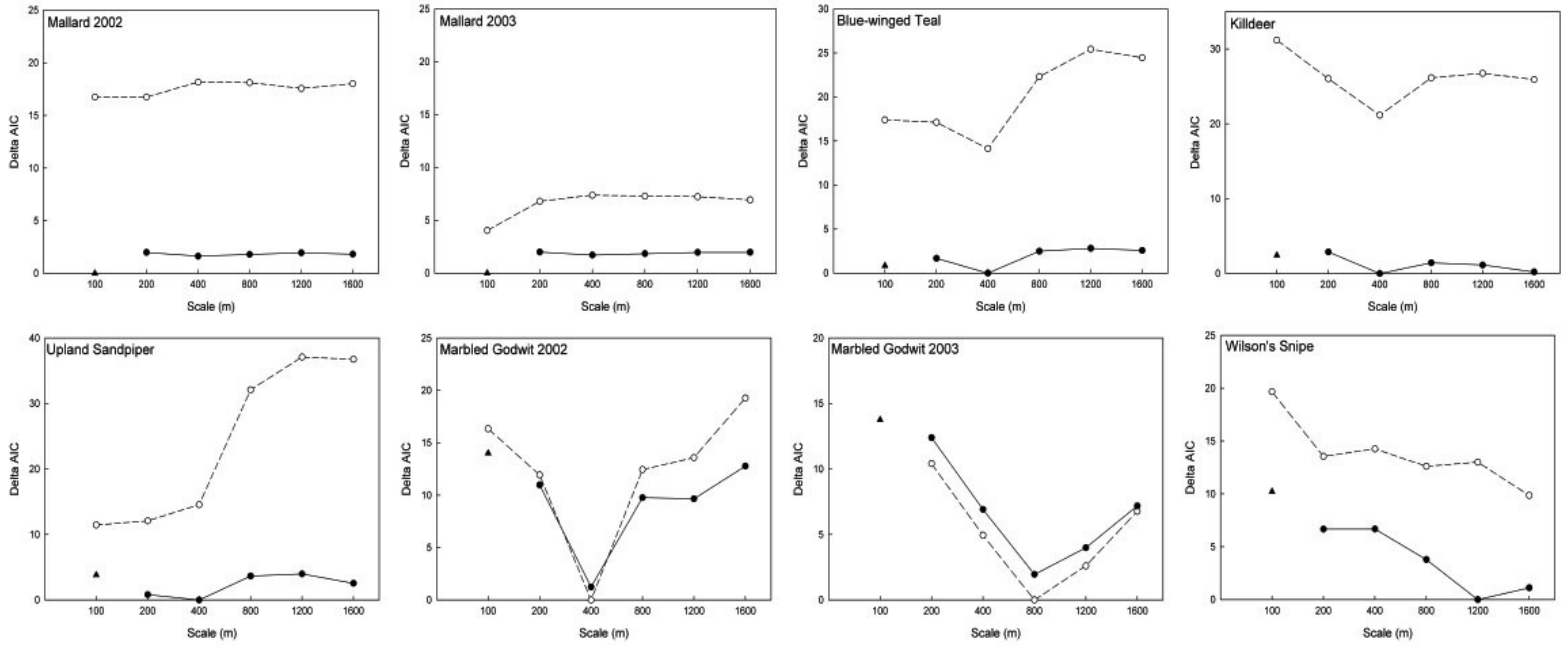
Plots of regression coefficient estimates and confidence intervals for estimates demonstrating the strength of tree cover effects across scales (*Ecological Archives* A016-039-A3).

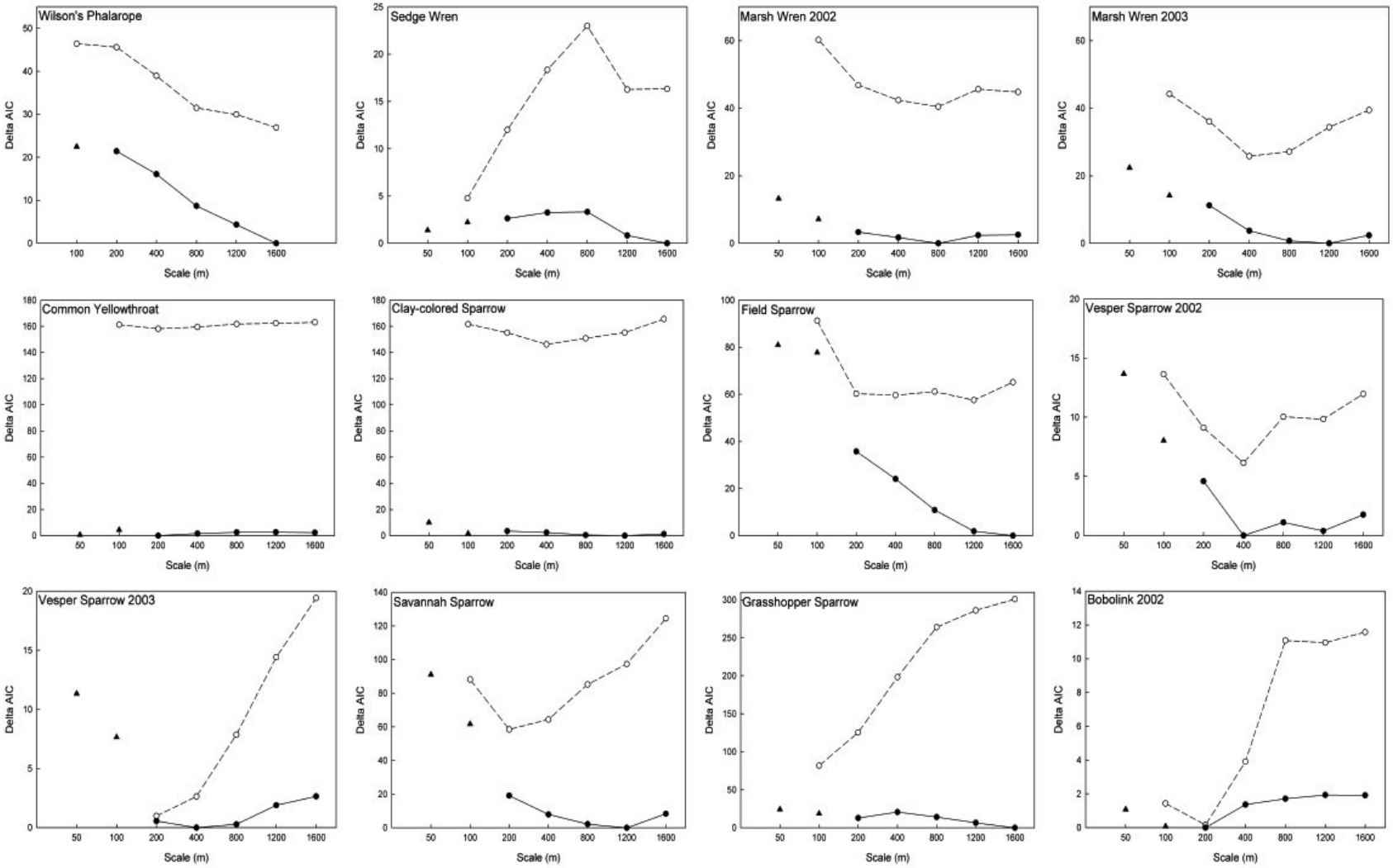
Ecological Archives **A016-039-A1**

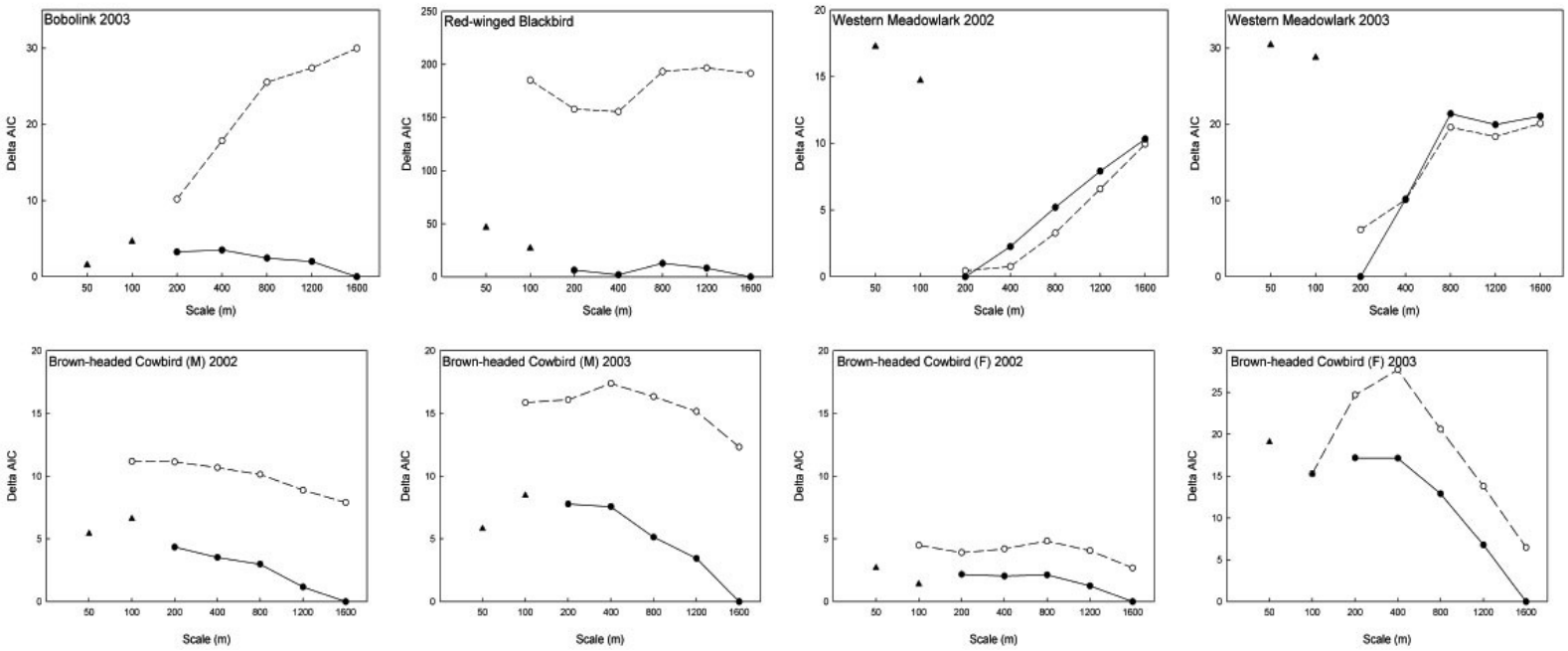
Mary Ann Cunningham and Douglas H. Johnson. 2006. Proximate and landscape factors influence grassland bird distributions. *Ecological Applications* 16:1062–1075.

Appendix A. Plots of ΔAIC show scales of response and comparisons between years, as well as comparisons between proximate, landscape, and combined models.

Graphs of ΔAIC compare models within a set. Best models have ΔAIC = 0, but models with ΔAIC < 3 can be considered competitive with the best model. Triangles indicate ΔAIC for proximate models. Dashed lines show ΔAIC across scales for models containing only year and one landscape variable (e.g., year + tree200). Solid lines show ΔAIC for combined (proximate and landscape) models at 200 to 1600 m scales. For proximate models, both 50-m and 100-m versions of the best model are shown where both were used.




Wilson's Phalarope
Sedge Wren
Marsh Wren 2002
Marsh Wren 2003
Common Yellowthroat
Clay-colored Sparrow
Field Sparrow
Vesper Sparrow 2002
Vesper Sparrow 2003
Savannah Sparrow
Grasshopper Sparrow
Bobolink 2002
Delta AIC
Scale (m)



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Ecological Archives **A016-039-A2**

Mary Ann Cunningham and Douglas H. Johnson. 2006. Proximate and landscape factors influence grassland bird distributions. *Ecological Applications* 16:1062–1075.

Appendix B. Summary of scales for which models are competitive for different species.

TABLE B1. Competitive proximate, landscape, and combined models: ΔAIC for best models at proximate and landscape scales is shown. Competitive models, here defined as ΔAIC < 3, are showns in bold typeface. For combined models, an "x" indicates scales at which a combined model had ΔAIC < 3.

Species	ΔAIC of best model		Scales (in m) with competitive combined models				
	Proximate	Landscape	200	400	800	1200	1600
Mallard (2002)	**0.0**	16.7	x	x	x	x	x
Mallard (2003)	**0.0**	6.8	x	x	x	x	x
Blue-winged Teal	**0.8**	14.1	x	x	x	x	x
Killdeer	**2.4**	21.2	x	x	x	x	x
Upland Sandpiper	3.8	12.1	x	x			x
Marbled Godwit (2002)	14.0	**0.0**		x			
Marbled Godwit (2003)	13.8	**0.0**			x		
Wilson's Snipe	10.2	9.9				x	x
Wilson's Phalarope	22.5	26.9					x
Sedge Wren	**1.4**	13.6	x			x	x
Marsh Wren (2002)	7.2	40.5		x	x	x	x
Marsh Wren (2003)	14.2	25.8			x	x	x
Common Yellowthroat	**0.6**	158.1	x	x	x	x	x
Clay-colored Sparrow	**1.6**	146.2		x	x	x	x
Field Sparrow	77.7	57.5				x	x
Vesper Sparrow (2002)	8.0	6.1		x	x	x	x
Vesper Sparrow (2003)	7.6	**2.6**	x	x	x	x	x
Savannah Sparrow	61.7	58.5			x	x	
Grasshopper Sparrow	18.7	125.6					x
Bobolink (2002)	**0.1**	**0.1**	x	x	x	x	x
Bobolink (2003)	**1.5**	10.2			x	x	x
Red-winged Blackbird	27.0	155.5		x			x
Western Meadowlark (2002)	14.7	**0.4**	x	x			
Western Meadowlark (2003)	28.8	6.2	x				
Brown-headed Cowbird (m) (2002)	5.4	7.9			x	x	x
Brown-headed Cowbird (m) (2003)	5.8	12.3					x
Brown-headed Cowbird (f) (2002)	**1.4**	**2.7**	x	x	x	x	x
Brown-headed Cowbird (f) (2003)	15.3	6.5					x

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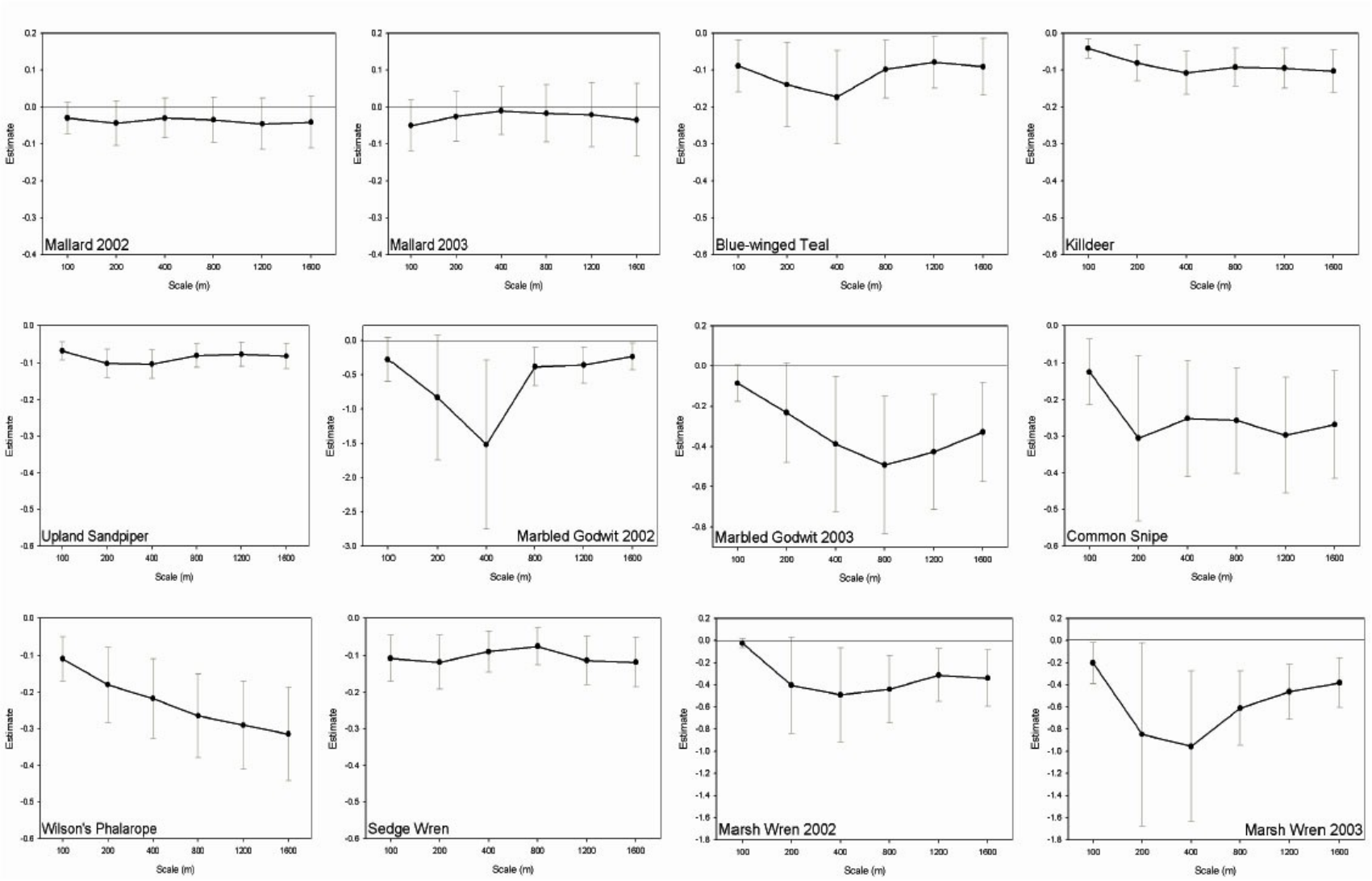
Ecological Archives **A016-039-A3**

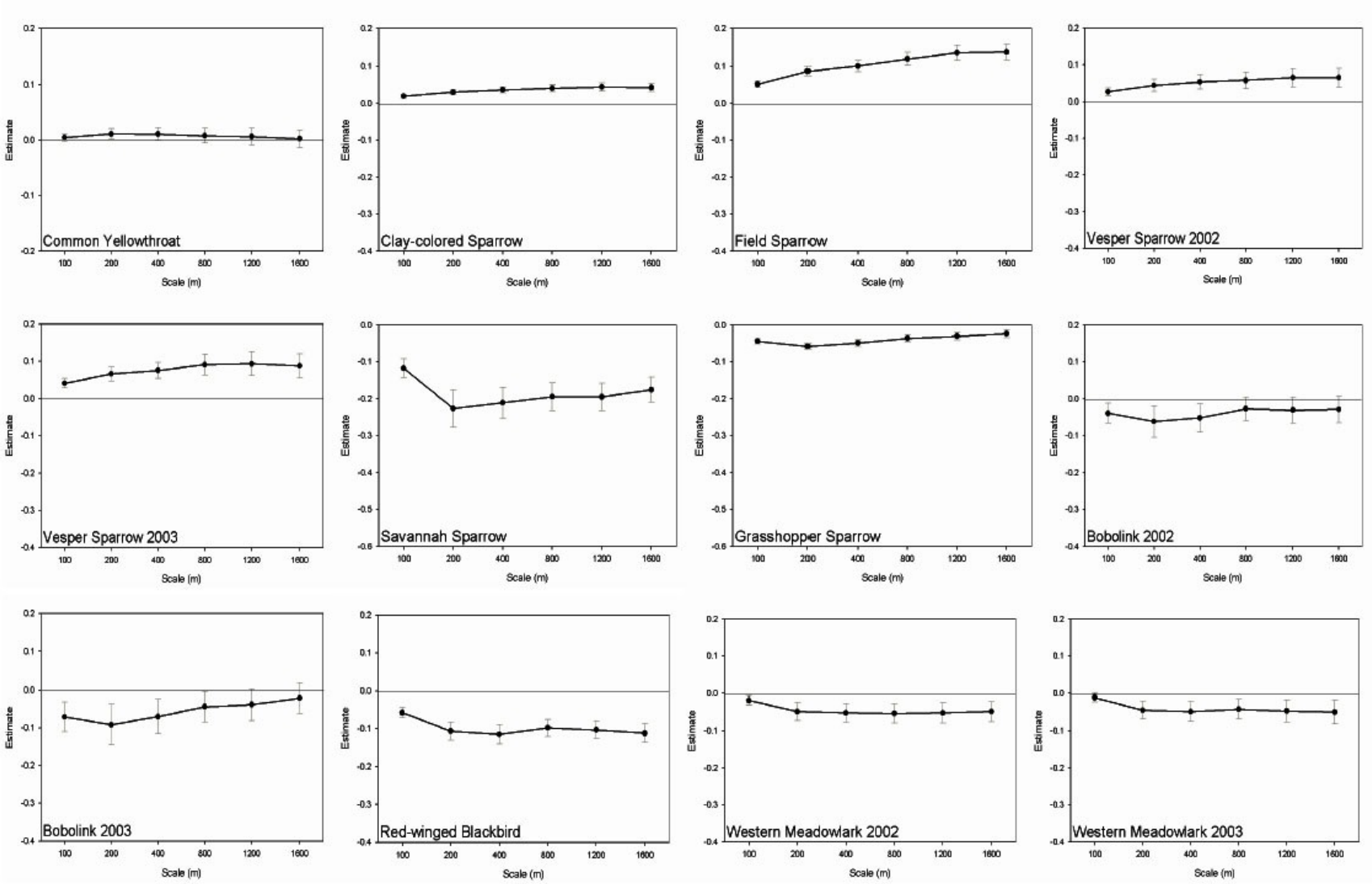
Mary Ann Cunningham and Douglas H. Johnson. 2006. Proximate and landscape factors influence grassland bird distributions. *Ecological Applications* 16:1062–1075.

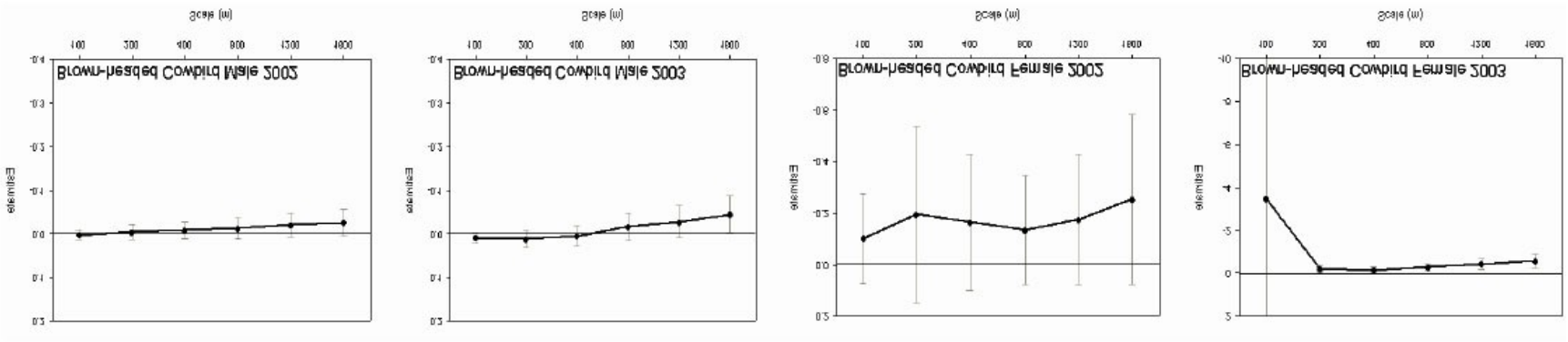
Appendix C. Regression coefficient estimates demonstrated the strength of tree cover effects across scales.

Regression coefficient estimates, with 95% confidence intervals, for tree cover at proximate scales (50 to 100 m) and landscape scales (200 to 1600 m). Coefficients are from the landscape-only models (e.g., year + tree200).

Regression coefficient estimates demonstrate the strength of tree cover effects across scales. Unlike AIC, the strengths of effects can be compared by the magnitude of parameter estimates, so the scale of vertical axes of graphs below is constant, except for a few species with large coefficients. Seven of the 19 species (Blue-winged Teal, Upland Sandpiper, Marbled Godwit, Marsh Wren, Savannah Sparrow, Grasshopper Sparrow, and Bobolink) had strongest responses at smallest scales (≤ 400 m). Five species (Wilson's Phalarope, Clay-colored Sparrow, Field Sparrow, Vesper Sparrow, and Brown-headed Cowbird) had stronger responses at the largest scales (1200-1600 m). Five species (Killdeer, Wilson's Snipe, Sedge Wren, Red-winged Blackbird, and Western Meadowlark) had relatively strong responses at both small and large scales, and two (Mallard and Common Yellowthroat) had negligible responses to tree cover at nearly all landscape scales. In general, scales that produced small ΔAIC values in landscape models (Appendix A) corresponded to the scales with large parameter estimates (below).


Mallard 2002
Mallard 2003
Blue-winged Teal
Killdeer
Upland Sandpiper
Marbled Godwit 2002
Marbled Godwit 2003
Common Snipe
Wilson's Phalarope
Sedge Wren
Marsh Wren 2002
Marsh Wren 2003
Estimate
Scale (m)
100
200
400
800
1200
1600


Common Yellowthroat
Clay-colored Sparrow
Field Sparrow
Vesper Sparrow 2002
Vesper Sparrow 2003
Savannah Sparrow
Grasshopper Sparrow
Bobolink 2002
Bobolink 2003
Red-winged Blackbird
Western Meadowlark 2002
Western Meadowlark 2003
Estimate
Scale (m)
100
200
400
800
1200
1600



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